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„Effects of landscape structure on the prey composition of the Long-eared Owl (*Asio otus*)“

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Zusammenfassung

Die Waldohreule (*Asio otus*) ist ein hochspezialisierter Räuber und allgemein für die Bildung von Winterschlafplätzen bekannt. Um mehr über die Faktoren herauszufinden, welche die Beutetierartenzusammensetzung dieser Eulenart, wie zum Beispiel die Landschaftsstruktur, Schlafplatzgröße und Geographie, beeinflussen, wurden während der Überwinterungssaison 2014/2015 an 17 verschiedenen Winterschlafplätzen in landwirtschaftlichen, suburbanen und urbanen Gebieten Österreichs insgesamt 2,763 Gewölle aufgesammelt und 14 Nagetierarten, 2 Spitzmausarten und 8 Singvogelarten nachgewiesen. Mit einem relativen, durchschnittlichen Anteil von etwa 80% pro Winterschlafplatz war die Feldmaus (*Microtus arvalis*) die mit Abstand am häufigsten genutzte Beutetierart. Die relative Häufigkeit der Feldmaus schwankte an den 17 Winterschlafplätzen zwischen 62 und 90%. Die Waldmaus (*Apodemus sylvaticus*) und die Zwergwaldmaus (*Apodemus uralensis*) wurden zu einem relativen, durchschnittlichen Anteil von 5.4% beziehungsweise 6.0% genutzt. Der Anteil anderer Beutetierarten war von noch geringerem Ausmaß. Die Auswertung der Daten ergab, dass (i) das genutzte Beutetierartenspektrum maßgeblich von der relativen Häufigkeit der Feldmaus beeinflusst wurde, (ii) zusätzliche Beutetierarten verstärkt bejagt wurden, wenn die Verfügbarkeit der Feldmäuse aus verschiedenen Gründen nicht gegeben war und (iii) die relative Häufigkeit der Feldmaus mit der Anzahl der Eulen an den Winterschlafplätzen bedeutend zunahm. Im Gegensatz dazu hatte die Anzahl der Eulen an den Schlafplätzen keinen Einfluss auf das genutzte Beutetierartenspektrum. Darüber hinaus konnten wir keine wesentlichen Auswirkungen der Landschaftsstrukturen auf den Nutzungsgrad der hauptsächlich genutzten Beutetierarten feststellen. Da die Veränderungen der Vegetation kaum Auswirkungen auf Häufigkeit der Feldmaus zu hatten, ist davon auszugehen, dass die Feldmaus offenbar in den Umgebungen aller Schlafplätze sehr häufig war. Unsere Daten deuteten ebenso darauf hin, dass die geographischen Unterschiede in Zusammensetzung der Beutetierarten zwischen den einzelnen Schlafplätzen in signifikantem Ausmaß auf die geographische Länge zu beziehen sind. Außerdem konnte diesbezüglich kein Zusammenhang zur Landschaftsstruktur nachgewiesen werden. Die Ergebnisse zeigten, dass bio-geographische Faktoren, wie zyklische Wühlmaus-Fluktuationen und naturräumliche Veränderungen in der Häufigkeit und der Diversität der Beutetierarten für den Klärungsbedarf an Unterschieden in den Proportionen der genutzten Beutetierarten maßgeblich von Bedeutung waren.

Schlagwörter: Beutetierzusammensetzung, Waldohreule, Gewölle, Winterschlafplätze, Beuteverfügbarkeit, Landschaftsstruktur, Nahrungsspektrum, Längengrad

ABSTRACT

As a highly specialized predator the Long-eared Owl (*Asio otus*) is commonly known for occupying wintering roosts. In order to learn more about factors shaping the prey species composition of this owl species, such as landscape structure, roost size and geography, a total amount of 2,763 pellets was collected during wintering season 2014/2015 at 17 different winter roosts in agricultural and suburban areas in Austria. In the pellets we found remains of 14 rodent, 2 shrew and 8 songbird species. As the prevailing species Common Vole (*Microtus arvalis*) dominated the feeding range with a medium share of nearly 80% per winter roost by far. Among the 17 wintering roosts the relative abundance of Common Vole fluctuated between 62 and 90 %. Ural Field Mouse (*Apodemus uralensis*) and Wood Mouse (*Apodemus sylvaticus*) were utilized at an average of 6.7% and 4.7% respectively, whereas additional food resources had only little importance. Data analysis yielded that (i) food niche breadth was widely affected by the relative abundance of Common Vole, (ii) when availability of Common Voles was denied for different reasons, additional prey species were remarkably preyed upon and (iii) the relative abundance of Common Vole significantly increased with the number of owls occupying a wintering roost. In contrast species richness wasn't diversified with increasing roost size. Moreover landscape features seemed to have no major impacts on the utilization of the main prey species. As Common Vole appears being barely affected by changes of vegetation, it might have been highly available in the surroundings of all studied winter roosts. Moreover our data indicated that geographical changes in the prey species composition between roost sites were significantly related to longitude, while again no relationship with landscape composition could be detected. The results therefore suggested that specific features of bio-geographic factors such as cyclic vole fluctuations and spatial shifts in abundance and diversity of the prey species were of greatest significance for explaining differences in the proportions of utilized prey species.

Key words: prey composition, Long-eared Owl, pellets, wintering roosts, prey availability, food niche breadth, landscape features, longitude

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Introduction

Although regarded as a dietary specialist preying on *Microtus* voles, the Long-eared Owl (*Asio otus*) adjusts its trophic regime on the local prey availability (Benedek & Sîrbu 2010, Birrer 2009, Gryz & Krauze-Gryz 2015, Maccarone & Janzen 2005, Mori & Bertolino 2015). Numerous studies revealed a significant bio-geographical pattern as well as a seasonal significance for differences of this nocturnal predator's diet. Furthermore this owl species is commonly known for its preference for hunting in open habitats (Milchev & Ivanov 2016, Sharikov & Makarova 2014, Tome 1994, Tulis *et al*. 2015a). The owl's preference for low-vegetated areas can be explained by a morphological aspect. Long wings as well as its airy wing-loading suggest the efficient adaption for hunting in open land characterized habitats (Marti 1976).

In Central Europe the Long-eared Owl preys mainly on mammals. It primarily feeds on rodents like voles (*Microtus* spp.) and mice (*Apodemus* spp., *Mus* spp.), but only little on rats, shrews and birds (Glutz von Blotzheim & Bauer 1994, Sharikov & Makarova 2014). Remains of Common Vole dominate the prey spectrum with 70.0% or more by far (Birrer 2009, Sharikov & Makarova 2014, Wijnandts 1984), as this species commonly occupies areas with scarce and low vegetation such as fields and meadows, habitats preferred by the Long-eared Owl for foraging (Birrer 2009, Nilsson 1981). The genera *Apodemus* spp. and *Myodes* spp. are commonly distributed in abundant vegetated, natural environments, in or near woods (Benedek, Sîrbu 2010, Birrer 2009, Nilsson 1981), whereas the genera *Mus* ssp. and *Rattus* ssp. are mainly found in pellets of owls hunting in urban and suburban areas. The positive relationship between the relative abundance of *Microtus arvalis* in the diet and the number of owls counted at winter roosts in Slovakia is additional indicating the importance of *Microtus arvalis* as prey of Long-eared Owls (Tulis *et al.* 2015a). Further, the absolute abundance of the main prey was proved being positively related to of number of owls at winter roosts (Sharikov *et al*. 2013).

The number of insectivores (3.5 %) and birds (12.0%) as well as the high percentage (37.0%) of *Microtus agrestis* in the British Islands can be explained by the absence of *Microtus arvalis* (Birrer 2009, Mikkola 1983). *Microtus oeconomus* is an important prey species in Northern Europe (Canova 1989, Nilsson 1981). In southern and southeastern regions of Europe birds (11.0% and 5.9%, respectively) represent an important component of the trophic regime of the winter diet of the Long-eared Owl (*Asio otus*) (Benedek & Sîrbu 2010, Birrer 2009).

Exceeding the dietary composition with a ratio of nearly 60% by far, the highest degree of bird predation of wintering Long-eared Owls was observed in Tulcea at the Danube Delta, Romania (SÁNDOR & KISS 2004). The authors explained the high proportion of birds as a result of the characteristic landscape structure. Situated at the mouth of Danube Delta, the study sites are dominated by floodplains and other wetlands. With seasonal water cover not secure for the hibernation of small rodents, the owls apparently shift to avian prey. Mammalian prey selection included shrews, rats and mice, but sparsely voles like *Arvicola terrestris* and *Microtus epirotocus*. This untypical prey selection caused by the unusual habitat conditions and the lack of *Microtus arvalis* illustrate the significance of landscape structure on the prey composition of the Long-eared Owl.

While *Apodemus agrarius* seems to be a frequent and alternative prey species in Romania, *Microtus savii* is commonly preyed upon in Italy (CECERE & VICINI 2000, SERACUSA *et al* 2015). As *Microtus arvalis* does not occupy southeastern Turkey, according to SEÇKIN & COŞKUN (2005) approximately 71.3 % of the dietary composition there consists of *Microtus guentheri*. Being abundant at a study site in Beytepe, Ankara, in northern Turkey, *Microtus arvalis* (44.4%) represents a fairly important dietary component among the recorded rodents, whereas *Apodemus* sp. illustrates an alternative rodent prey species with a frequency of 25% (TURAN 2005). While *Microtus* voles represent the dominate food source in Central Europe, reptiles and invertebrates with 5.4 % and 21.1 % of the recorded prey items seem to be a crucial food source of North African populations (BIRRER 2009). Accordingly geographical differences in prey occurrence and abundance seem to have substantial impacts on the feeding composition of this nocturnal hunter.

Further, also urbanization appears to effect prey composition. For example, the winter diet of Long-eared Owls from two urban and suburban roosts at Beijing, China consisted mainly of bats and birds, while rodents played only a minor role (LI *et al*. 2007, TIAN *et al*. 2014). The increasing urbanization did not only change the foraging habitats and the landscape composition. Causing a decline of the owl population, the lack of rodents as a consequence of habitat loss may also have forced owls to shift to other prey. The high abundance and availability of bat species were attributed to the loss of secure hibernation sites in old buildings and bats therefore changed to less suitable places like tree holes (ZHAN *et al*. 2005), both affected by real estate expansion as well as the lack of conservation.

Agricultural intensification and artificial environments as well as the loss of landscape heterogeneity, fragmentation and devastation of natural habitats have significantly increased throughout the last decades. Even though this owl species is listed as Least Concern in the IUCN Red List, its appearance is assumed to be declining (BIRDLIFE INTERNATIONAL 2012), as these significant changes in landscape structures most likely strongly affected prey availability for Long-eared Owls (ASCHWANDEN *et al*. 2005). However, effects of landscape structure on the dietary composition of the Long-eared Owls have been scarcely explored.

The aims of this study were to (i) investigate the current trophic regime of wintering Long-eared Owls in Austria along an longitudinal gradient in order to record spatial variation, (ii) to analyze to what extent the landscape structure around winter roosts affects prey species composition and (iii) finally how this is related to the size of winter roosts.

Material and methods

Study areas

Pellets of Long-eared Owls were collected during the winter 2014/2015 at seventeen different winter roosts distributed across five states of Austria, i.e. Vorarlberg, Upper Austria, Lower Austria, Vienna and Burgenland 2014/2015. All seventeen studied winter roosts (R_1-R_{17}) of Long-eared Owls were located in the lowlands of western, northern and eastern Austria, situated between the very eastern locations of Burgenland at approximately 120 m above sea level to the most western part of Vorarlberg at 400 m above sea level.

Fig. 1: Location of studied Long-eared Owl winter roosts in Austria

Providing secure shelter for the Long-eared Owl from predators, evergreen trees such as Scots Pine (*Pinus sylvestris*), Common Spruce (*Picea abies*) as well as fir (*Abies* spp.) and thuja (*Thuja* spp.) are commonly used for wintering (Wijnandts 1984). Roosting trees of this study also comprised broadleaf trees like poplar (*Populus* spp.) and Weeping Willow (*Salix babylonica*). As roost R_9 in northern Burgenland was abandoned during the progress of winter it was therefore not further considered in this study. The number of owls at the 17 remaining winter roosts varied from 2 to approximately 60 individuals. In accordance with other studies the number of owls at the studied winter roosts increased during the course of the winter (Sharikov & Makarova 2014, Wijnandts 1984).

Study sites R_1 (48°17'44.7"N 16°26'13.3"E) and R_2 (48°08'38.8"N 16°26'57.1"E) are both located in communal cemeteries of Vienna, the capital city of Austria and represent small winter roosts. R_1 is located in the outskirts of Vienna in the former village Stammersdorf (188 metres above sea level) and the roost is surrounded by garden settlements and intensive farming areas, whereas R_2 is located in the vast mosaic of woodlots, trees and meadows of Vienna Central Cemetery, encircled by sealed areas of urbanization.

Roosts investigated in Lower Austria were of intermediate size. R_3 (48°03'53.6"N 16°22'17.2"E) is situated in the palace gardens of Laxenburg castle. Embedded in the vast mosaic of woods and meadows of this landscape garden on the one hand and intensively used farming areas and suburban settlements on the other, the trees used for roosting are located on two islands situated in a water body. One of these roosts is inaccessible and one open to the public (Franzensburg Island). Pellets were only collected on Franzensburg Island. At study site R_4 (48°23'50.2"N 16°05'40.1"E) owls were roosting at a communal cemetery of village Hausleiten on the ridge of Wagram hill (207 meters above sea level), embedded in intensively used agricultural areas and garden settlements. Being the most northern of all the study sites analyzed, R_5 (48°32'49.5"N 16°45'39.1"E) represents a mid-sized roost sheltering up to 15 owls in a suburban environment, surrounded by garden settlements, wood lots and agricultural open land. R_6 (48°08'12.1"N 16°28'56.8"E) is situated in a park with single Scots Pines (*Pinus sylvestris*) used for wintering and is enclosed by garden settlements, fields, wood lots and small forests. Moreover highways and industrial, sealed areas are located in the immediate vicinity.

Study site R_7 (48°05'40.3"N 17°03'32.3"E) is located at Kittsee Castle and was occupied by two Long-eared Owls roosting in single Douglas firs (*Pseudotsuga menziesii*). Kittsee Castle and its well wooded gardens are surrounded by the village of Kittsee, agricultural land and woodlots. The other eight roosts investigated in northern Burgenland are located in the region of Seewinkel at the eastern side of Lake Neusiedl, which geologically belongs to the Pannonian Plain. With the Biological Station of Illmitz nearby, the roost R_{11} (47°46'09.9"N16°46'01.2"E) is located in the conservation area of the National Park Neusiedler See – Seewinkel, in the proximity of Lake Neusiedl and surrounded by reed beds, vast meadows and salt marshes, salt ponds and pastures, with the local habitat hutweide being predominant in this European salt steppe. The roosts R_8 (47°44'47.2"N 16°49'45.3"E) and R_{10} (47°51'22.3"N 16°49'40.6"E) are located inside the mosaic of patchy protected areas of the National Park Neusiedler See – Seewinkel, but the areas of the roost sites do not have on own conservation status. Both winter roosts are situated in the suburban environments of the villages Apetlon and Podersdorf am See. In Apetlon the owls roosted in single thujas (*Thuja* spp.) at a communal cemetery at the margin of intensively cultivated fields and the settlement. In Podersdorf am See they occupied a single weeping willow (*Salix babylonica*) in a garden located in the village center with Lake Neusiedl nearby. Study site R_{12} (47°47'16.6"N 16°54'41.2"E) is situated in a garden settlement in the immediate vicinity of the salt pond Zicksee at St. Andrä and inhabited by approximately 20-40 owls, whereas roost R_{13} (47°43'26.2"N 16°56'05.0"E) sheltered about ten owls, wintering in single Scots pines (*Pinus sylvestris*) in the communal cemetery of Wallern, a small village surrounded by vast intensive managed fields. Roost R_{14} (47°52'59.7"N 16°56'08.6"E) with a maximum of >60 owls is located in a courtyard of the spa house Marienkron at the margin of the village Mönchhof. This winter roost is surrounded by a mosaic of meadows, woodlots, forests, suburban environment and conventional agriculture. At study site R_{15} (47°56'57.5"N 16°56'32.9"E) near the village Zurndorf owls were roosting in Scots pines (*Pinus sylvestris*) of a well wooded garden settlement embedded in an area of intensive farming.

The roost R_{16} (48°11'41.3"N 14°46'07.0"E) in Upper Austria is located in the vicinity of the river Danube and enclosed by meadows, fields, hedges and lots of single trees, since flooding events have destroyed the local village *Eizendorf an der Donau* more than a decade ago. The two study sites R_{17} (47°24'01.2"N 9°39'49.4"E) and R_{18} (47°28'36.3"N 9°41'29.5"E) in Vorarlberg are situated at nearly 400 metres above sea level in (i) a little forestation of Scots pines and (ii) in a suburban garden settlement, both surrounded by humid meadows, drainage channels and fields near Lake Constance and the Alter Rhein, an old riverbed of the river Rhine.

Sampling design

To account for seasonal variation in the diet, owl pellets were sampled at all seventeen winter roosts at monthly intervals in the end of November 2014, the end of December 2014 and the end of January 2015. All roosts were completely searched for pellets during each survey, in order to prevent collecting pellets older than one month. The time frame of ten days for each sampling round, organized in field trips on pre-defined routes, was determined to guarantee similar weather conditions. In total 2,763, whole and well preserved pellets were collected under all trees occupied by owls within a radius of two meters measured from the stem.

Table 1: Information on sampled winter roosts.

Roost	Latitude	Longitude	Altitude (m asl.)	Max. number of counted owls	Collected pellets			Sum
					Nov. 2014	Dec. 2014	Jan 2015	
R1	**48°17'44.7"N**	**16°26'13.3"E**	**188**	**2**	37	25	45	**107**
R2	**48°08'38.8"N**	**16°26'57.1"E**	**177**	**4**	50	40	41	**131**
R3	**48°03'53.6"N**	**16°22'17.2"E**	**117**	**15**	73	40	50	**163**
R4	**48°23'50.2"N**	**16°05'40.1"E**	**207**	**15**	49	40	60	**149**
R5	**48°32'49.5"N**	**16°45'39.1"E**	**177**	**15**	63	71	70	**204**
R6	**48°08'12.1"N**	**16°28'56.8"E**	**162**	**20**	63	60	60	**183**
R7	**48°05'40.3"N**	**17°03'32.3"E**	**138**	**2**	29	24	37	**90**
R8	**47°44'47.2"N**	**16°49'45.3"E**	**120**	**40**	65	66	66	**197**
R10	**47°51'22.3"N**	**16°49'40.6"E**	**121**	**20**	79	50	55	**184**
R11	**47°46'09.9"N**	**16°46'01.2"E**	**117**	**12**	47	31	49	**127**
R12	**47°47'16.6"N**	**16°54'41.2"E**	**116**	**40**	57	75	51	**183**
R13	**47°43'26.2"N**	**16°56'05.0"E**	**120**	**11**	78	70	60	**208**
R14	**47°52'59.7"N**	**16°56'08.6"E**	**131**	**60**	65	50	44	**159**
R15	**47°56'57.5"N**	**16°56'32.9"E**	**137**	**15**	46	70	50	**166**
R16	**48°11'41.3"N**	**14°46'07.0"E**	**242**	**8**	52	70	66	**188**
R17	**47°24'01.2"N**	**9°39'49.4"E**	**400**	**8**	55	50	55	**160**
R18	**47°28'36.3"N**	**9°41'29.5"E**	**400**	**5**	45	66	53	**164**
TOTAL					**953**	**898**	**912**	**2,763**

Fieldwork comprised several parts, i. e., the collection of pellets, the counting of owls and characteristics of the vegetation, such as the position, number and species of trees used for roosting.

Sample preparation and determination of pellets' dry weight

Pellets were stored in sealed envelopes with date of collection, and roost ID, and then frozen. For further analysis the samples were dried in a drying oven at 40°C for at least two till seven days depending on their wetness at the moment of collection. Determining the pellet's dry weight with an analytical balance is a valid method used to provide an insight into digestive efficiency and hunting success of this nocturnal predator. Measurements taken were conducted with an analytical balance (Ohaus Adventurer AR0640).

Determination of prey remains

For further analysis the pellets were dissected using standard techniques and tools, i. e., a magnifier, a pair of forceps, dissection needles, sliding caliper and a little brush (MÄRZ 1987, YALDEN 2012). Skeletal fragments of mammalian prey items, i. e., lower jaws, skulls and teeth were identified to the species level using taxonomic keys (JENRICH ET AL. 2012). Bird remains were determined at species level with the aid of the ornithological collection of the Zoology Department of the Natural History Museum Vienna. Feathers sometimes gave further indication. The number of prey individuals was counted as most frequent skull element.

Impacts of landscape structure on the dietary composition

In order to test for effects of landscape structure on diet composition, determining the owls' home range is crucial. According to a fundamental study in the Netherlands (WIJNANDTS 1984) the total home range in autumn, winter and spring is amounted to a mean of 2,025 ha (min.-max.: 1,136-2,560 ha). However, only a small part of 185-370 ha (ca. 10-20 %) of this home range area is used intensively for foraging. Not regarding season, a survey in Switzerland evaluated home range sizes of approximately 980 ha(HENRIOUX 2000), while an average home range size during non-breeding season of 504.8 ha was recorded for Long-eared Owls in the plains of River Po (GALEOTTI *et al*. 1997). A radio telemetry based study on Crete reported utilized home range sizes of 498-1768 ha (EMIN 2015). Furthermore the average home range during non-breeding season of Long-eared Owls in a Slovakian study comprised sizes between 469.9 and 446.9 ha, whereas no significant differences in utilization between breeding and non-breeding season could be detected (TULIS *et al*. 2015b).

In the present study we therefore quantified landscape structure within a radius of 500 meters around winter roosts, as this represents the average intensively exploited home range of wintering long-eared owls (WIJNANDTS 1984). To digitalize landscape structures on available satellite images (Google maps 2016), we used the software QGIS (version 2.18.4.).

ROMANOWSKI & ZMIHORSKI (2008) conducted their analysis in Central Poland using three main habitat types, i. e., permanent grasslands (meadows and pastures), open areas (abandoned land and arable fields) as well as forest habitats, whereas EMIN (2015) identified seven main land cover categories for his investigation of habitat selection of the long-eared owl in the agricultural characterized environment of Crete, Greece: annual crops, olive plantations, vineyard, irrigated vegetable fields, phrygana, residential and artificial (both sealed, built-up areas). Further a Slovakian study based on telemetry considered nine land units (woodlands, park vegetation, built-inhabited area, gardens, linear-wood vegetation, water units, meadows, arable land and forest edges) and revealed units of arable land to be the predominant landscape structure in the recorded home ranges, whereas woodlands and forest edges represented lesser abundant land units (TULIS *et al*. 2015b).

A North Italian survey considered eight types of habitat(network habitats, rice fields, other crops, mature woods, young poplar groves, uncultivated fields, farmhouses & wide traffic roads and water bodies (rivers and wide canals) in the plains of River Po. The analysis of the habitat use of radio-tracked Long-eared Owls yielded that they had mainly preyed in uncultivated fields (primarily fallows) and ecotonal narrow habitats like field edges, verges of trees and rural roads, as these network habitats inhabit high densities of prey species. Furthermore non-breeding owls mostly utilized treelines, which presumably represent perches for hunting (GALEOTTI *et al*. 1997).

Considering up previous studies the following nine main types of landscape components were recorded for land cover classification in the present study: open land (agricultural utilization), meadow, shrub, woodlot, single tree, water body, garden settlement, sealed area and bare ground.

Fig. 2: Example for digitalized landscape structure parameters at study site R_{13} via QGIS (version 2.18.4). Different colors indicate agricultural areas (violet), bare ground (fuchsia), garden settlements (turquoise), meadows (green), sealed areas (pink), shrubs (brown), single trees (aqua) and woodlots (yellow).

Using the percentage coverage of habitat types, the Shannon diversity index (H) was applied to quantify landscape diversity, whereas smaller values indicate relatively poor landscape habitat diversity, high values represent increased habitat diversity around the studied winter roosts.

Data analysis

To test for effects of landscape structure on the richness of utilized prey species, the number of prey species recorded in pellets from individual winter roosts was used as response variable. As the number of recorded prey species was neither significantly related to the size of the winter roost nor to the numbers of pellets sampled at winter roosts (see Results section), other richness measurements were not calculated.

All measured variables were tested for multicollinearity, before examining the effects of landscape variables on prey species richness using a GLM approach. If variables were strongly correlated, either only those variables with a higher relevance for foraging Long-eared Owls were further considered or different GLMs not including both variables simultaneously were calculated. Moreover variables of only minor variance were not considered in calculated GLMs in order to avoid an overparametrization of models. GLMs were calculated with a normal error distribution and a log-link function using the software IBM SPSS Statistics version 20. Wald statistics were calculated for the GLMs for the purpose of detecting univariate effects of landscape variables on prey species richness.

In order to detect relationships between prey species composition and landscape composition and longitude, respectively, Spearman matrix rank correlations were calculated using the software Primer 5 for Windows version 5.2.9. While similarities of landscape composition and prey species composition, respectively, between roost sites were quantified as Bray-Curtis similarities, Euclidian distances were used for quantifying differences in roost sites' longitude. Similarity matrices for prey species composition were calculated including and excluding *Microtus arvalis*, respectively. Finally, similarity relationships in prey species composition between roost sites were illustrated in a NMDS (non-metric multidimensional scaling) ordination.

As the CCA (canonical correspondence analysis) ordination is a multivariate narrowed method to obtain substantial gradients among declarative variables in a record, this ordination technique was computed for visualizing to what extent the relative abundance of prey species at roost sites is related to certain landscape features.

Pearson correlations were applied for gaining further insights into the effects of roost size, or more specifically, the maximum number of counted owls, on the mean number of *Microtus arvalis* individuals per pellet and its relative importance as food of owls at roosts, respectively. Furthermore the effects of landscape features on *Microtus arvalis* individuals per pellet and the species' relative abundance in pellets, respectively, were considered using GLMs (with normal error distribution and log-link function). We once again applied a Pearson correlation to assay if the mean number of *Microtus arvalis* individuals per pellet is related to the percentage of individuals of other prey species in the dietary composition recorded at roost sites.

RESULTS

Diet variability

In 2,763 pellets a total of 3,484 vertebrate prey specimens belonging to 24 prey species were recorded at winter roosts of Long-eared Owls, including 14 rodent, 2 shrew and 8 songbird species. Invertebrates were not represented in the digestive composition. The predominant prey species *Microtus arvalis* (n=2288) exceeded the trophic regime with a medium share of 80% of all prey items by far. Its absolute proportion fluctuated between 62-90 % among the seventeen study sites. Except of *Apodemus uralensis* with 6.7 % of all identified prey individuals, all other species contributed less than 5 % (Fig. 3). Also the mean relative abundance of *Microtus arvalis* per roost was close to 80 % (Fig. 4).

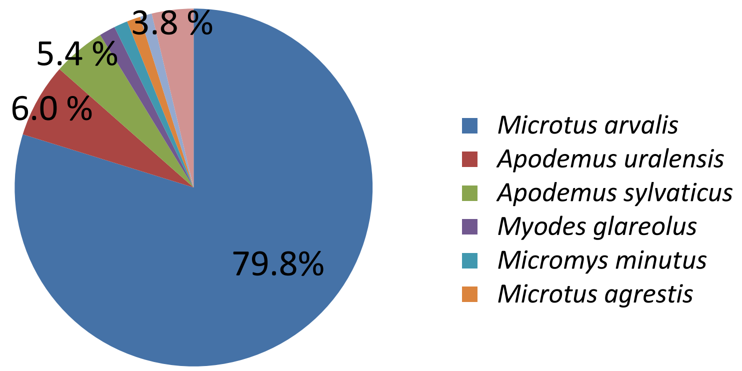

Figure 3: Relative abundance of prey species utilized by Long-eared Owls at winter roosts.

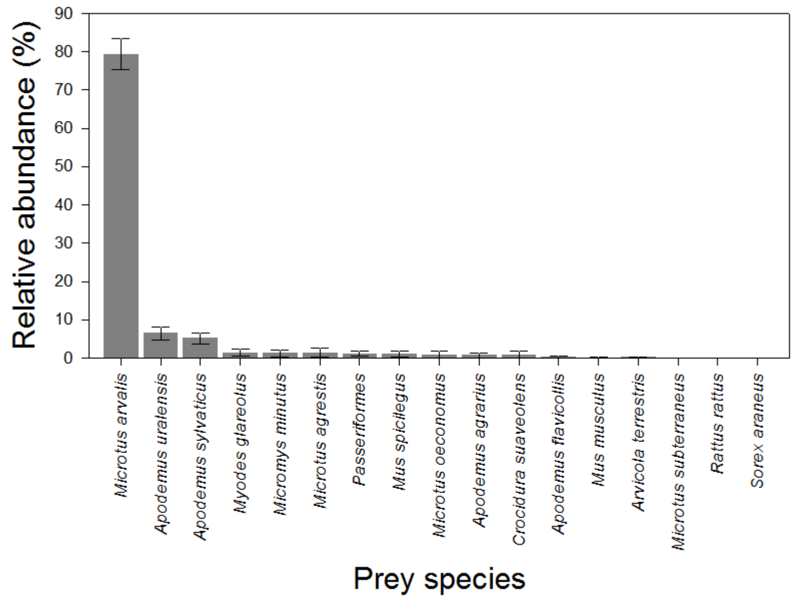

Figure 4: Mean relative abundance (± 95% CI) of recorded prey species per winter roost. Recorded songbirds are pooled as "Passerifomes".

A total of 11.4% of the prey remains in the present study consisted of Ural Field Mice (*Apodemus uralensis,* n=270) and Wood Mice (*Apodemus sylvaticus*, n=256). Mammalian prey species recorded only occasionally in the pellets were among others Striped Field Mouse (*Apodemus agrarius*, n=37), Bank Vole (*Myodes glareolus*, n=68), Field Vole (*Microtus agrestis,* n=55), Steppe Mouse (*Mus spicilegus*, n=42), Tundra Vole (*Microtus oeconomus*, n=40), Eurasian Harvest Mouse (*Micromys minutus*, n=38). Only scarcely abundant species comprised Lesser White-toothed Shrew (*Crocidura suaveolens*, n= 17), Yellow-necked Mouse (*Apodemus flavicollis*, n=15), Water Vole (*Arvicola terrestris*, n=7), House Mouse (*Mus musculus*, n=7), Common Pine Vole (*Microtus subterraneus*, n=3), Black Rat (*Rattus rattus*, n=3), and Common Shrew (*Sorex araneus*, n= 1). Avian prey comprised the prey species Blue Tit (*Cyanistes caeruleus*, n=18), Great Tit (*Parus major*, n=12), Marsh Tit (*Parus palustris*, n=3), European Goldfinch (*Carduelis carduelis*, n=2), European Greenfinch (*Carduelis chloris,* n=1), European Robin (*Erithacus rubecula*, n=1), Eurasian Wren (*Troglodytes troglodytes*, n=1) and Goldcrest (*Regulus regulus*, n=1) as well as three individuals of Tits, which could not be further determined (*Parus* sp.), yielding a total amount of 42 prey individuals.

Richness of used prey species: effects of roost size

Between six and twelve prey species could be recorded per winter roost with an average (± SD) of 8.24 (± 1.99) prey species. Recorded prey species richness was not related to maximal number of counted owls per roost site ($r = 0.08$, $p = 0.7609$) and the number of collected pellets ($r = 0.28$, $p = 0.2679$).

Richness of used prey species: effects of landscape structure

The features of the landscapes around the studied roost sites differed strongly (Table 2). Of the habitat types only bare ground and single shrubs and trees (%) were not further considered as both only covered a very small proportion of all studied landscapes (Table 2). Because the percentage of sealed areas and areas of settlements and gardens correlated strongly ($r = 0.828$, $p < 0.0001$), we only considered the habitat type "settlements and gardens" in all further analyses as it may be more important as foraging habitat for Long-eared Owls. Since the habitat type "open land" is strongly correlated with the variable "landscape diversity" we calculated two GLMs testing for effects of the remaining landscape variables, one not including "open land" and a second not including "landscape diversity". In the first GLM woodland cover proved being significantly related to prey species richness (Table 2), which declined with increasing woodland cover (Fig. 5).

Table 2: Landscape features of the studied roost sites. Variables considered in further analyses are indicated by a grey background.

Landscape variables	Mean	Minimum	Maximum	SD
Landscape diversity (Shannon Wiener H)	1.38	0.92	1.60	0.17
Edge length (km)	97.73	53.35	155.23	27.01
Bare ground (%)	1.72	0.10	5.45	1.77
Garden settlement (%)	23.83	0.44	52.04	15.91
Meadows (%)	7.12	0.10	42.64	13.09
Open land (agricultural areas, meadows) (%)	36.63	10.08	78.68	19.70
Sealed areas (%)	10.29	0.00	24.44	7.78
Shrubland (<50% trees) (%)	3.32	0.05	9.51	2.53
Single shrubs and trees (%)	0.96	0.28	2.14	0.62
Water bodies (%)	7.32	0.00	37.72	12.41
Woodlots (%)	8.82	0.24	54.49	13.23

Table 3: Results of GLMs testing for effects of landscape variables on richness of used prey species, including (a) landscape diversity and (b) open land as additional predictor variables.

(a)

Parameter	B	SE	95% Wald CI		Hypothesis Test		
			Lower	Upper	Wald Chi-Square	df	*p*

(Intercept)	2.388	0.262	1.874	2.901	83.106	1	<0.001
Landscape diversity	-0.056	0.406	-0.850	0.739	0.019	1	0.891
Edge length	-0.002	0.002	-0.006	0.002	1.233	1	0.267
Garden settlement	0.002	0.005	-0.008	0.012	0.180	1	0.672
Meadows	0.004	0.003	-0.001	0.010	2.763	1	0.096
Shrubland (<50% trees)	-0.020	0.022	-0.063	0.023	0.869	1	0.351
Waterbodies	0.007	0.005	-0.002	0.017	2.181	1	0.140
Woodlots	-0.010	0.004	-0.017	-0.003	6.961	1	0.008

(b)

Parameter	B	SE	95% Wald CI		Hypothesis Test		
			Lower	Upper	Wald Chi-Square	df	*p*
(Intercept)	2.617	0.839	0.973	4.261	9.734	1	0.002
Openland	-0.002	0.008	-0.017	0.013	0.097	1	0.755
Edge length	-0.003	0.002	-0.006	0.000	2.965	1	0.085
Garden settlement	-0.002	0.011	-0.022	0.019	0.026	1	0.871
Meadows	0.002	0.007	-0.011	0.016	0.109	1	0.741
Shrubland (<50% trees)	-0.026	0.017	-0.060	0.007	2.352	1	0.125
Waterbodies	0.004	0.008	-0.012	0.021	0.247	1	0.619
Woodlots	-0.013	0.008	-0.028	0.003	2.558	1	0.110

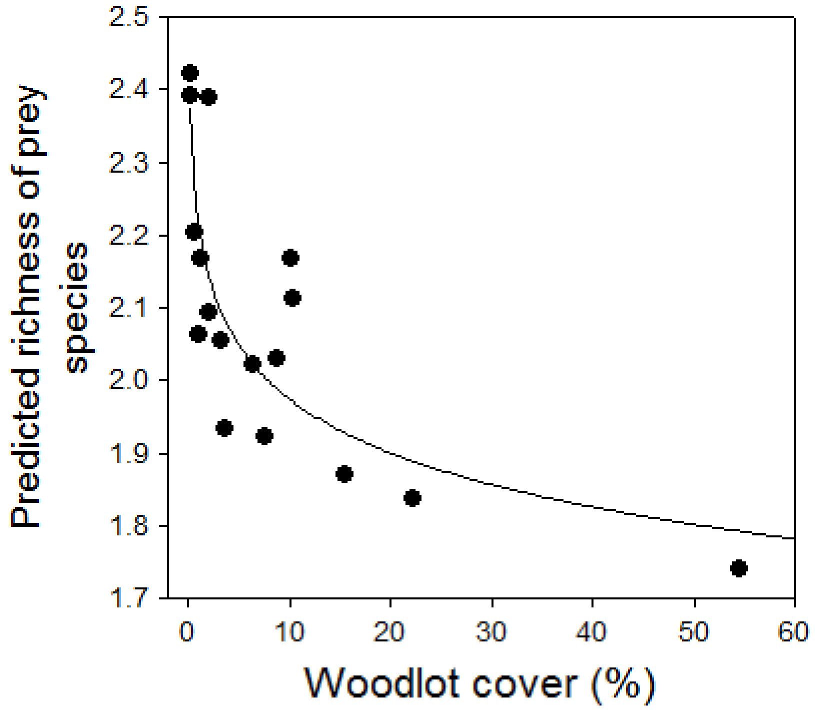

Figure 5: Relationship between richness of prey species utilized by Long-eared Owls and woodlot cover as predicted by a GLM (Table 2a).

Effects of landscape structure and geography on the composition of utilized prey

Calculated Spearman matrix rank correlations did not indicate any effects of landscape composition on prey species composition (*Rho* = -0.168, $p = 0.902$). In contrast, changes in prey species composition between roost sites were significantly related to longitude (*Rho* = 0.314, $p = 0.022$). This effect was even stronger when excluding the most abundant prey *Microtus arvalis* (*Rho* = 0.425, $p = 0.001$), while again no relationship between prey species and landscape composition could be detected (*Rho* = -0.050, $p = 0.667$). The conspicuous geographical shift in prey species composition is also visible in the two NMDS ordinations based on Bray-Curtis similarities including (Fig. 6a) and excluding *Microtus arvalis* (Fig. 6b).

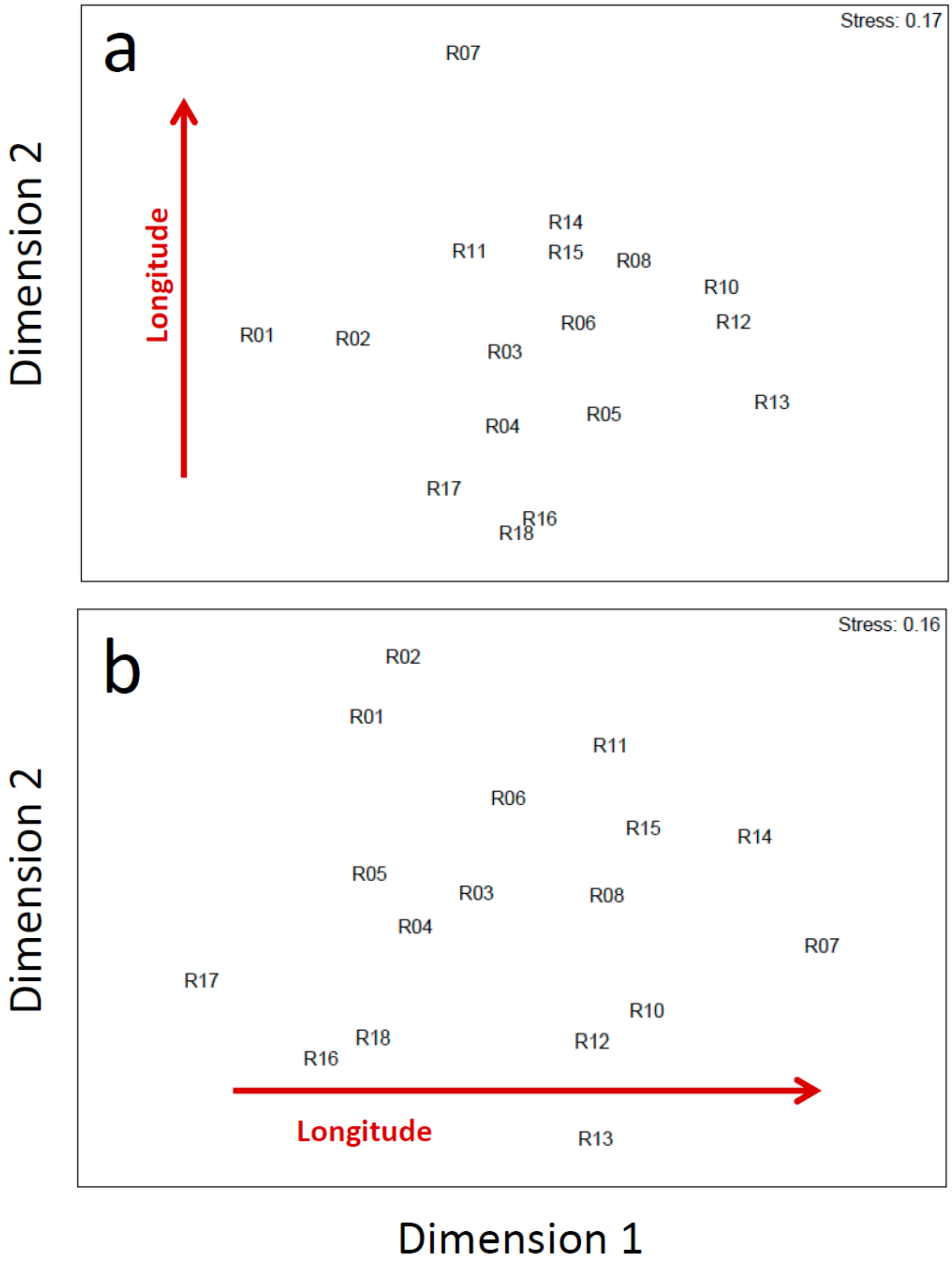

Figure 6: NMDS ordinations visualizing similarity relationships (quantified using Bray-Curtis similarities with square-root transformed abundances) in prey species composition between roosting sites (a) including and (b) excluding *Microtus arvalis*. Red arrows indicate changes in prey species composition explained by longitudinal differences between roost site locations.

The two axis of the CCA ordination explain 28.6% of the variance in the prey species data, and 67.9% of the species-environment variation. The most common prey species *Microtus arvalis* is plotted in the center of the ordination plot, emphasizing that this rodent species appears being largely unaffected by changes in landscape composition and hence is highly available in all landscapes surrounding the studied Long-eared Owl winter roosts. *Crocidura* *suaveolens* occurs particularly at roost sites embedded in landscapes with a high cover of gardens/settlements. The occurrence of other species in pellets appears to be positively affected by increasing cover of water bodies (*Microtus oeconomus*), woodlots (*Microtus agrestis*) and meadows (*Arvicola terrestris*) (Fig. 7).

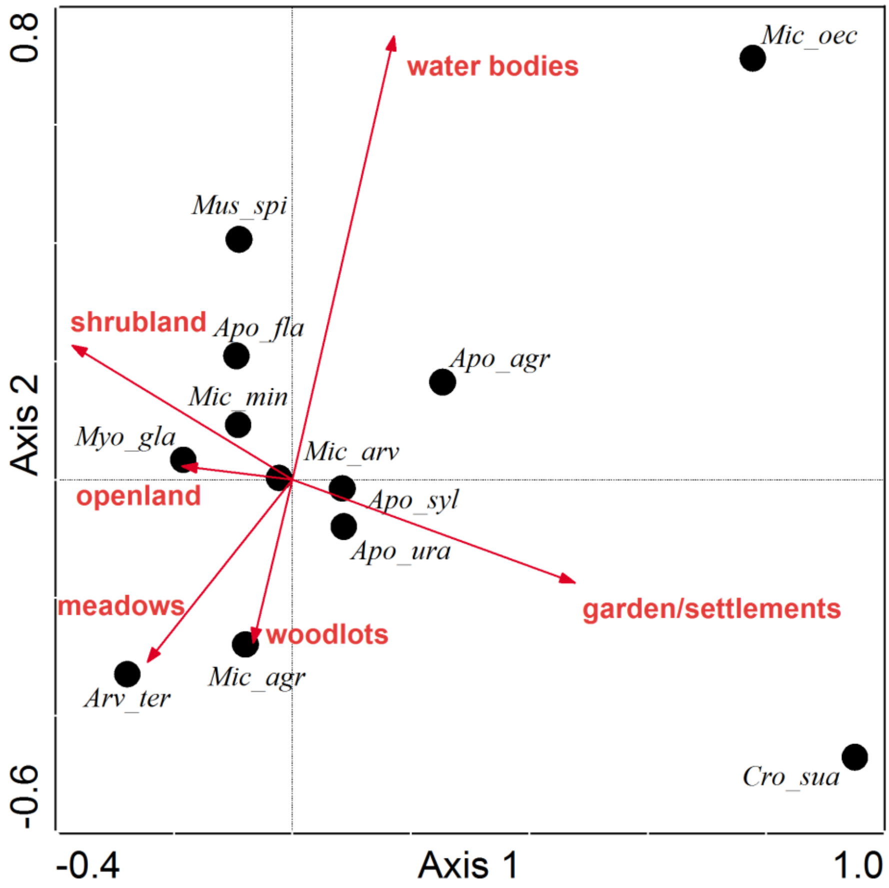

Figure 7: CCA ordination with habitat variables as vectors and the relative abundance of prey species as points. Codes of prey species: *Apo_agr = Apodemus agrarius, Apo_fla = Apodemus flavicollis, Apo_syl = Apodemus sylvaticus, Apo_ura = Apodemus uralensis, Arv_ter = Arvicola terrestris, Cro_sua = Crocidura suaveolens, Mic_min = Micromys minutus, Mic_agr = Microtus agrestis, Mic_arv = Microtus arvalis , Mic_oec = Microtus oeconomus, Mus_spi = Mus spicilegus, Myo_gla = Myodes glareolus*.

Effects of roost size and landscape structure on mean number of *Microtus arvalis* individuals per pellet

A mean (± SD) of 1.52 (± 0.28) *M. arvalis* individuals per pellet was found per roost site, with a recorded mean minimum and maximum of 1.05 and 1.94 individuals per pellet, respectively. The mean number of *M. arvalis* individuals per pellet increased significantly with increasing roost size ($r = 0.602$, $p = 0.0105$; Fig. 8) and its relative importance as food of owls at different roosts (r = 0.774, p = 0.0003; Fig. 9). Remarkably, calculated GLMs testing for effects of landscape features on *Microtus arvalis* individuals per pellet and the species' relative abundance in pellets did not indicate any significant relationship (results not shown).

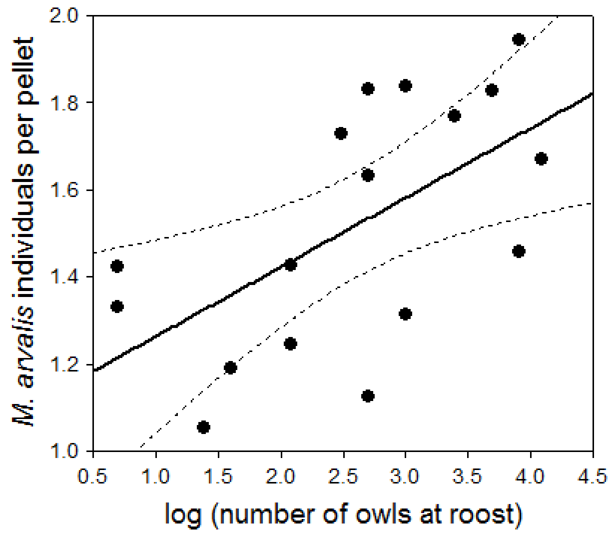

Figure 8: Relationship between number of *Microtus arvalis* individuals per pellet and roost size.

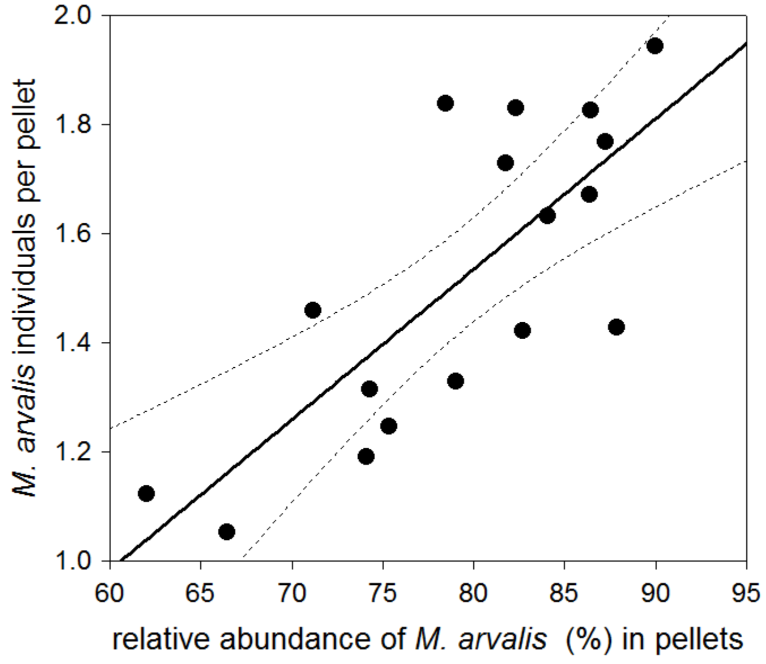

Figure 9: Relationship between number of *Microtus arvalis* individuals per pellet and the species relative abundance as prey in analyzed pellets at different roost sites.

When the mean number of *Microtus arvalis* individuals per pellet is decreasing this is apparently compensated by an increasing percentage of individuals of other prey species in the food composition recorded at roost sites (r = - 0.774, p = 0.003; Figure 10).

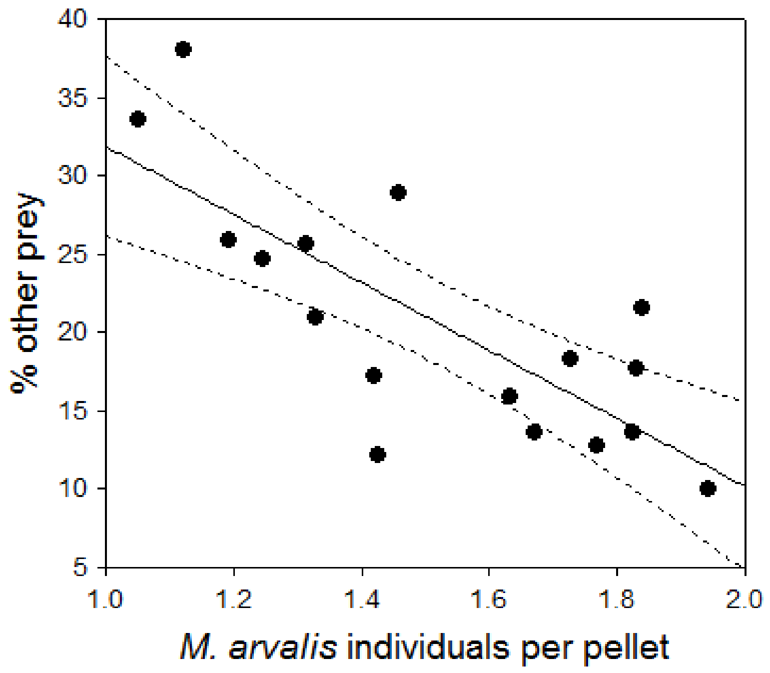

Figure 10: Relationship between number of *Microtus arvalis* individuals per pellet and the percentage of individuals of other prey species at roost sites.

Discussion

Utilized prey species: an Austrian perspective

In the present study Common Vole (*Microtus arvalis*) dominated the diet of Long-eared Owl (*Asio otus*) with a medium share of 80% of all utilized prey species, whereas other prey species were of minor importance. These results fully corresponded with the findings from studies from Slovakia, Slovenia, Northern Italy as well as the Netherlands, where values in similar proportions to those of our study have been recorded (Wijnandts 1984, Sergio *et al*. 2008, Tome 2009, Tulis *et al*. 2015a). Occasionally utilized prey species recorded in our study comprised Ural Field Mouse (*Apodemus uralensis*) and Wood Mouse (*Apodemus sylvaticus*) as well as Field Vole (*Microtus agrestis*), Tundra Vole (*Microtus oeconomus*), Bank Vole (*Myodes glareolus*), Harvest mouse (*Micromys minutus*), Steppe Mouse (*Mus spicilegus*) and Striped Field Mouse (*Apodemus agrarius*). Tome (2009) recorded higher portions of European Pine Vole (*Microtus subterraneus*) and Water Vole (*Arvicola terrestris*) in Slovenia, which were both scarcely preyed upon in the present study, but similar proportions of Wood Mouse and Harvest Mouse. Wood Mouse was recorded at all studied winter roosts, while Ural Field Vole was only found at all winter roosts in Lower Austria, Vienna and Burgenland. These results can be explained by the fact, that Ural Field Vole reaches the western end of its Palearctic distribution in the Pannonian Basin (Grimmberger & Rudloff 2009). That Field Vole, European Pine Vole, Water Vole and Striped Field Mouse are only rarely utilized as prey by Long-eared Owls, as recorded in this study, can be explained by the species' preference for moist, high-grass microhabitats and its diurnal activity, respectively (Grimmberger & Rudloff 2009, Korpimäki 1992, Thissen *et al*. 2015). Kitowski (2013) recorded high amounts of Common Vole (nearly 75%) and minor scales of Tundra Voles (4.1%) in Poland, whereas the records of another Polish pellet analysis yielded an even higher amount of Tundra Voles (22.36-28.04%) and large scales of Common Voles (55.70-66.59%). Also the records of Bank Voles were of similar proportions (1.27-5.21%) (Stasiak *et al*. 2014).

Owl pellet analyses can contribute substantial information to assess the current distribution and conservation status of small mammals. For example, our data provide important faunistic records of the Steppe Mouse (*Mus spicilegus)* at all study sites located in Burgenland. It prefers grassy steppe, verges of orchards, tree avenues as well as grassy waysides and field edges across Eastern Europe. Throughout the last decades it has suffered significant declines in number and distribution by means of habitat loss, agricultural intensification and increased herbizide application (UNTERHOLZNER *et al*. 2000). All records of Steppe Mouse from our study were located within the species' known distribution range. In Austria its appearance in Austria is restricted to areas of northern Burgenland. There it reaches it most eastern distribution range in the area of Parndorf Plain and Seewinkel in the eastern and northern vicinity of Lake Neusiedl. (GRIMMBERGER & RUDLOFF 2009, UNTERHOLZNER *et al*. 2000). Moreover the region of Seewinkel represents an isolated area of Tundra Vole's (*Microtus oeconomus*) northern Holarctic range and inhabits its subspecies Pannonic Root Vole (*Mictorus oeconomus mehelyi*), which can be found in Austria, Hungary and Slovakia (THISSEN *et al*. 2015). The rather big vole is commonly known for being a glacial relict preferring wet meadows with sedges. In the end of the 19^{th} century the presence of Pannonic Root Vole around Lake Neusiedl was larger-scaled than today. Furthermore it was considered to be plausibly distributed near Fischamend (Lower Austria) too (REBEL 1933, THISSEN *et al*. 2015). This suggests that Tundra Vole might have suffered from agricultural intensification as well. Appearances have only been verified for the region of Seewinkel and the west side of Lake Neusiedl later on (BAUER 1953, THISSEN *et al*. 2015). In our study Pannonic Root Vole was recorded at three study sites, being most abundant in St. Andrä (n=29) and Podersdorf (n=8) at the east side of Lake Neusiedl. In our study Striped Field Mouse (*Apodemus agrarius*, n=37) was recorded at all 8 study sites located in Burgenland, being most abundant in the most eastern of all investigated study areas, in Wallern (R_{13}: n=18). In Austria Striped Field Mouse has only rarely been documented in the area east of Lake Neusiedl (Burgenland), in southeastern Styria (SACKL *et al*. 2007) and once in northern Lower Austria up to now, but this neobiota's expansion is considered of having developed in the recent years. As its wide distribution range spreads from northern Europe (Finland, Denmark and the middle of Germany) over the Czech Republic and Slovakia and finally borders Austria in eastern Burgenland and southeastern Styria, our records of Steppe mouse are in compliance with the species' known distribution (GRIMMBERGER & RUDLOFF 2009, LAUERMANN *et al*. 2011). Proportions of Field Vole (*Microtus agrestis*, n= 55) in the prey composition increased towards the west of Austria although this prey species was represented in all investigated states of Austria. This is in correspondence with available literature too (GRIMMBERGER & RUDLOFF 2009, WALDER & VORAUER 2013).

The recorded predominant proportion of *Arvicolinae* and the marginal amount of avian prey, respectively, is in compliance with literature. KORPIMÄKI (1992) explained the large scales of Arvicolinae in central and northern areas of Europe as a result of their high availability and the lack of other suitable prey species. Birds comprised only a minor proportion of the utilized prey composition in central, northern and northeastern Europe (SERGIO *et al*. 2008, STASIAK *et al*. 2014, TOME 2009, TULIS *et al*. 2015a). KITOWSKI (2013) related the proportion of utilized bird species in Europe to a latitudinal gradient and many study revealed an increase in the proportion of utilized avian and (insectivorous) species (BENEDEK & SÎRBU 2010, GALEOTTI & CANOVA 1994, GARCIA *et al*. 2005, HERRERA & HIRALDO 1976, KIAT *et al*. 2008, MILCHEV *et al*. 2003), PIROVANO *et al*. 2000, SÁNDOR & KISS 2004, 2008) the more southwards we advance.

Effects of roost and landscape features on richness of utilized prey species

Our results clearly indicated that prey species richness did not increase with increasing roost size (TULIS *et al*. 2015a). As already mentioned, the predicted prey species richness dropped with increasing woodlot coverage to a moderate extent. Even though Long-eared Owls tend to prefer hegdes, isolated trees and edges of woodlots and copses as raised stands (HENRIOUX 2000, MARTINEZ & ZUBEROGOITIA 2004), they avoid hunting inside woodlots (HOLT 1997). Hence the remaining profitable hunting area around roosts is decreasing with increasing woodlot cover. These findings may be explained by a pattern of ecology, which is commonly known as species-area relationship (SAR) (PRESTON 1962, ROSENZWEIG 1995): whereas larger areas tend to comprise a wider spectrum of inhabiting species, the number of participated prey species is in decline, when only diminutive areas remain for preying by reason of substantial proportions of woodlot cover.

While some authors emphasized the opportunistic predation of the Long-eared Owl (MIKKOLA 1983, TULIS *et al*. 2015a), others claimed the substantially high proportion of Common Voles to be affected by the owls' accessibility to their preferred main prey species (BIRRER 2009). However, many studies revealed the abundance of lesser preyed species in the field being not regarded, unless the decline of the amount of the main prey species dictates so (KORPIMÄKI & NORRDAHL 1991, TOME 2003, 2009, TULIS *et al*. 2015a). To conclude, there have been discussions whether the abundance of Common Voles in the field correlates with its availability or whether availability of Common Vole is opposed by the relative accessibility of the owls to their predominant participated food source. Several factors may influence the accessibility of Common Vole (BIRRER 2009), such as snow cover (CANOVA 1989, JEDRZEJEWSKA & JEDRZEJEWSKI 1998, WIJNANDTS 1984), vegetation structure (ASCHWANDEN *et al*. 2005), rainfall (ROMANOWSKI & ZMIHORSKI 2008) and wind (SHARIKOV & MAKAROVA 2014). TOME (2000) referred to another factor influencing the accessibility of the most abundant prey species, as this study recorded substantial differences in size between individuals of a certain prey species seized by Long-eared Owls and potential prey individuals captured by applying traps. Accordingly differences in the sizes of the prey species as well as prey individuals had major impacts on the attractiveness of the potential prey to the predator.

Several studies across different continents revealed the abundance of the main prey species being reflected by its availability in the foraging habitats and therefore argued that Long-eared Owls show a highly opportunistic foraging behavior (, LEADER *et al.* 2008, MATSUOKA 1974, MIKKOLA 1983). In a review about prey selection of Long-eared Owls in North America and Europe *Microtus* voles represented the main prey in 31 of 42 studies considered and comprised the dietary range from 29.8-94.4% (MARTI 1976, NILSSON 1981). At a winter roost in Kansas all determined rodent species except of House Mouse (*Mus musculus*) have been recorded by means of live-trapping methodology in similar proportions as represented in pellet analysis. The main prey species (Hispid Cotton Rat, *Sigmodon hispidis*) comprised more than 75% with only one vole species (Eastern Wood Rat, *Neotoma floridana*) being additionally abundant in the foraging habitat (MACCARONE & JANZEN 2005).

Effects of landscape features on the prey composition

The reviewed results confirm the widespread view that the Long-eared Owl provides a rather high tolerance towards changing landscape composition, as in our study landscape structure didn't have any detectable effects on the richness and composition of the used prey species. Besides MIKKOLA (1983) and LEADER *et al*. (2008) another study substantiated this nocturnal predator's preference for open land character (arable fields and meadows), as the obtained home ranges of the tracked owls emphasized the high utilization of open land units (TULIS *et al*. 2015b). Furthermore we agree with EMIN (2015) and MARTÍNEZ & ZUBEROGOITIA (2004) that the owl is well adjusted to a changing degree of habitat openness, because in our study the Common Vole comprised 62-90% despite pronounced differences of open land cover (ranging between 10.08 and 78.68%) between winter roosts.

Although the relative abundance of some prey species was apparently affected by the varying spatial cover of habitat types around winter roosts our study did not indicate any strong effects of landscape structure on prey composition of the Long-eared Owl. These findings can be explained by the overall predominant importance of Common Vole as prey species. For instance, in our study area the Tundra Vole, a glacial relict with a Holarctic distribution known for preferring moist meadows and damp tundra, was found predominantly in the vicinity of water bodies. Accordingly our results are in compliance with literature (GRIMMBERGER & RUDLOFF 2009). Moreover the occurrence of Water Vole (*Arvicola terrestris*), Field Vole (*Microtus agrestis*) and Lesser White-toothed Shrew (*Crocidura suaveolens*) seemed to be positively affected by increasing cover of meadows, woodlots and garden settlements, respectively. Accessibility to Water Vole is widely denied because of diurnal activity. Therefore this prey species was only poorly represented in the diet of Long-eared Owls in our study.

Effects of geography on prey composition

In the present study diet composition showed remarkable differences between roost sites along the longitudinal gradient. This could be caused by spatial differences in cyclic fluctuations of the Common Vole (SHARIKOV & MAKAROVA 2014, TOME 1994, 2009), which are again can be related to limiting factors of prey populations, such as the availability of food resources, microclimate conditions, parasitism and diseases (BEGON *et al*. 2006) Moreover it has been yielded in various studies that this already mentioned periodicity shows differences when related to different geographic areas. Whereas vole cycles of *Microtus arvalis* in Slovenia and northern England lasted for five years (TOME 2009) and three to four years, respectively (OLI 2003), Scandinavian surveys revealed durations of three to five years (KORPIMÄKI & NORRDAHL 1998, OLI 2003).

Moreover bio-geographical conditions have to be considered playing substantial roles concerning the latitudinal change in prey species composition in the present study. Prey composition of two study sites in the outskirts of Niigata City were compared with those of other pellet analyses of three different localities in Japan, yielding substantial differences concerning the main prey species. The most participated prey species differed among the study sites in relation to the types of vegetation as well as the bio-geographical regions. While the study site located in the plain of Ishikari River on Hokkaido Island (MATSUOKA 1974) is mostly covered by sub-boreal coniferous forests, with broadleaved deciduous forests also being abundant, the study sites on Honshu Island located in the vicinities of Niigata City and Osaka as well as the study site in Ehime, Shikoku Island, are located in the warm temperate zone and are therefore vegetated by broadleaved evergreen forests. Together all three vegetation types are represented at the five study sites. These represent two of three bio-geographic regions of Japan. While mammal assemblages on Hokkaido Island are almost similar to those of the adjacent Asian continent, endemic species are prevalent in the fauna of the Hondo area (comprises the islands Shikoku, Honshu and Kyushu) (MILLIEN-PARRA & JAEGER 1999). Hence the dominant prey species differed among the study sites (*Clethrionomys rufocanus* – Hokkaido, *Mus musculus* – Osaka, *Mus musculus* – Ehime, *Microtus montebelli* – Niigata, *Microtus montebelli* – Niigata). These results indicated that bio-geographical pattern of the respective habitat predefined the abundance of the main food source in the home range (CHIBA *et al*. 2005)

In addition a fundamental study explaining the existence of geographical shifts in trophic ranges compared food-niche changes across communities of sympatric owl species in northern Europe (Finland, Norway and Sweden), Central Europe (German, northern France) and western Europe (southern Spain). Methods of food utilization in North and Central Europe are rather restricted and so many predatory species in North and Central Europe primarily harvest on highly abundant microtines. In Mediterranean regions the widespread appearance of insects has evolved an accumulation of species specialized on feeding insects. As a result food utilization has been diversified there and so the group of microtine-feeding species as well as the high populations of *Microtus* voles breaks down. To conclude, the extant differences were associated with the spatial shifts in abundance and diversity of the prey species (HERRERA & HIRALDO 1976).

Another aspect of bio-geographical influence on predatory shifts is illustrated in a study from Israel, where the abundance of the main prey (*Gerbillus* spp.) was related on the conditions of soil (sandy (63-70%), sandy-loess (43%), loess-dominated (17%)). If soil condition didn't show any sandy characteristics, the genus *Gerbillus* was widely superseded by *Meriones* spp. (LEADER *et al*.2008). However, the rodent genera composition showed remarkable differences among the seven study sites. Where the genera *Gerbillus* and *Meriones* did not represent the main prey species, the dietary range was primarily comprised by House mice (*Mus musculus*) and Brown rats (*Rattus rattus*). The high abundance of commensal rodents (>50%) could be related to a mice plague at the study site of Sde Boqer as well as to the suburban environment of the study site located near Beer Sheva (LEADER *et al*.2008). Hence, these findings illustrate that the sudden expansion of a mice population is able to explain geographical differences in prey utilization.

In our study substantial shifts among the abundance of prey species in pellets are striking. Ural Field Mouse (*Apodemus uralensis,* n=42) was only recorded in pellets at winter roosts located in the Pannonian Basin. Therefore our results are in accordance with literature, as it reaches its most western distribution in Austria and the Czech Republic (GRIMMBERGER & RUDLOFF 2009). Striped Field Mouse (*Apodemus agrarius*, n=37) only occurred in pellets at study sites located in Burgenland, being most abundant in the most eastern study area of all investigated winter roosts in Wallern (R_{13}: n=18), as this region belongs biogeographically to the Pannonian region (according to bio-geographical region boundaries, not national borders). Steppe Mouse (*Mus spicilegus*, n=42) only occurred in study sites of Burgenland. Its recorded distribution in Austria is restricted to areas east and north of Lake Neusiedl, as it reaches it most eastern distribution range in the area of Parndorf Plain and Seewinkel in the eastern vicinity of Lake Neusiedl (GRIMMBERGER & RUDLOFF 2009, UNTERHOLZNER *et al*. 2000). Although represented at 10 roosts in all investigated states of Austria, the proportions of Field Vole (*Microtus agrestis*, n= 55) in the prey composition increased along the longitudinal gradient towards the west of Austria. While Field Vole was hardly preyed upon at roosts located in Burgenland (R_{12}: n=3, R_{13}: n=4), Lower Austria (R_3: n=2, R_4: n=3, R_5: n=1), and Vienna (R_1: n=2, R_2: n=1) the numbers of Field Voles in Upper Austria (R_{16}, n=18) and Vorarlberg (R_{17}: n=6, R_{18}: n=15) were of greater importance, as it prefers wet and cool climate and suitable habitats like meadows, woodland verges, marshes and upland moors (GRIMMBERGER & RUDLOFF 2009, WALDER & VORAUER 2013). To conclude, our results once more emphasize that the proportions of certain prey species in the diet of Long-eared Owls are illustrating their abundance in the foraging habitat.

The importance of *Microtus arvalis* as prey: effects of roost size and landscape structure

Our results did not indicate any substantial relationships between changes in landscape composition and the mean number of *Microtus arvalis* individuals per pellet as well as the species' relative abundance in pellets, respectively. According to BIRRER (2009) several other factors like weather, behavior and condition of the individuals, season and geographic location remain to have major influence on the accessibility of prey animals.

However, our results demonstrate that the Common Field Vole's importance as prey remained broadly unaffected by changes in landscape structure. Several surveys across different continents proved that the extent of utilization of the main prey species is reflecting their availability in the foraging habitats, hence emphasizing the opportunistic hunting behavior of Long-eared Owls (*Asio otus*) (LEADER *et al.* 2008, MATSUOKA 1974)

In order to gain insights into the relationship of a certain habitat type and its mammal assemblages, a comparison of the prey utilization and species richness of sympatric owl species with similar habitat requirements seems informative. A study carried out at six locations in southeastern Poland explained the broader dietary range of Barn Owls (*Tyto alba*) (H=2.44 overall diversity, B = 3.89 food niche breadth) in comparison with that of Long-eared Owls (H=1.734, B= 1.948) as a result of the high overlapping of their trophic range (total prey overlap 83.2%) (KITOWSKI 2013). That is considered to positively influence the coexistence of these sympatric owl species (MARKS & MARTI 1984). While the proportion of Common Voles in the diet of Long-eared Owls comprised an extent of nearly 75%, Barn Owls utilized this prey species only at a scale of approximately 27%. Long-eared Owls preyed mostly on *Microtus* spp. (81.8%) and *Apodemus* spp. (11.5%). Barn Owls frequently utilized *Microtus* spp. (31.4%), shrews (55.7%) and *Apodemus* spp. (5.6%) instead. Even though both owl species prefer open land for hunting, there are spatial differences. Barn Owls tend to prey in moist meadows without woodlots and are appreciative of buildings nearby, whereas Long-eared Owls prefer arable fields and a moderate extent of woodlots as well as single trees and hedgerows (KITOWSKI 2013). Taking into consideration that the Barn Owl is the least specialized of all owl species distributed in Austria (THISSEN *et al*. 2015), these differences may indicate also that the Long-eared Owl shows besides its overall opportunistic hunting behavior particular preferences for the Common Vole (*Microtus arvalis*).

Because of the already raised, guaranteed accessibility to Common Voles the overall prey composition was only slightly affected despite variational values of habitat openness and landscape structures. In accordance with SERGIO *et al*. (2008) and SHARIKOV *et al*. (2013) we can therefore confirm that the number of Long-eared Owls at wintering roosts is positively correlated with increasing availability of Common Voles. In contrast the decline of the owls' main food source was substantially compensated by the presence of lesser abundant species in pellets and therefore affected food niche breadth (MILCHEV *et al.* 2003, MILCHEV & IVANOV 2016, SERGIO *et al*. 2008, TOME 1994, 2009, TULIS *et al*. 2015a).

Further prospects

For future studies the effects of landscape structure on the dietary composition of the Long-eared Owl shall not be investigated just by studying the change of landscape composition within potential home ranges of individuals at winter roosts. Instead or additionally landscape preferences and utilization of the vicinity of the roost sites have to be observed using techniques that explore the duration and the degree of utilization. According to EMIN (2015) the context of landscape, respectively the proportion of utilized landscape structure, seemed to be more important than single categories of land cover. He therefore advised radio-telemetry tracking with high frequencies of temporal data collection as a crucial method for observing habitat preference and habitat utilization, as this knowledge may give further insights into the dietary composition of this nocturnal hunter. Additionally we recommend applying live-traps in order to formulate precise determinations concerning the proportion of the main prey species in relation to other abundant prey species in the field.

Another aspect suggested having impacts on the accessibility of Common Vole may be wind speed, the depth of snow cover (CANOVA 1989, ROMANOWSKI & ZMIHORSKI 2008, SHARIKOV *et al*. 2013) and the interaction of both, because high winds as well as snow layer would narrow the possibility for locating and obtaining prey individuals. Furthermore an increasing snow cover of more than 10-15 cm minimizes the possibility for Long-eared Owls to prey on Common Voles, as voles are commonly known for burrowing tunnels under the blanket of snow (JEDRZEJEWSKA & JEDRZEJEWSKI 1998, ROMANOWSKI & ZMIHORSKI 2008). Therefore we highly recommend methods concerning precipitation measurements, especially wind speed and snow fall, for further investigations.

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